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Direct Effects of Elevated CO_2 on Forest Tree Productivity

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Introduction

The concentration of CO_2 in the atmosphere has risen by approximately 35% since the pre-industrial era to approximately 380 ppm, now, and is continuing to rise by 1-2 ppm per year. This rate of CO_2 increase in the atmosphere is unprecedented in the recent past, for at least two million years. Despite the thousands of papers that have been published on the impacts of CO_2 on forest trees and forest ecosystems, how forest trees, the largest terrestrial carbon pool on Earth, will respond to the continued rise in atmospheric CO_2 is still largely unknown (Körner *et al.*, 2005), partly because the vast majority of research on the effects of elevated CO_2 has been carried out on small trees in laboratory or chamber conditions, in which the artificial nature of the exposure conditions make predictability to forest conditions questionable. Over the past decade, however, the development of Free-Air-CO_2-Enrichment (FACE) technology has allowed the exposure of entire forest stands of any age "*in situ*" with unaltered climatic conditions, realistic competitive interactions, and with natural pest interactions (Karnosky *et al.*, 2001; Figure 1). In this brief paper, we will examine recent results from FACE experiments that have addressed the question of rising atmospheric CO_2 effects on forest productivity and we will highlight remaining major knowledge gaps.

Forest Productivity Drivers

The question remains as to whether or not forest productivity will change as CO_2 rises in the atmosphere. Since most forest trees are not CO_2-saturated, photosynthesis has generally been shown to increase in elevated CO_2. While some down regulation has been reported under elevated CO_2, long-term FACE studies have not detected any major photosynthetic acclimation (Karnosky *et al.,* 2003; Liberloo *et al.,* 2006). Another key factor driving forest productivity is the leaf area carried by the trees. Leaf area index (LAI), a common measure of leaf area in forest stands, has been generally enhanced by elevated atmospheric CO_2 (Karnosky *et al.,* 2003, 2005; Liberloo *et al.,* 2006) in young stands but not in older stands (Asshoff *et al.,* 2006). The duration of foliage, the time from bud break to leaf abscission, also appears to be sensitive to elevated atmospheric CO_2, but responses have been variable from no effect (Asshoff *et al.,* 2006; Moore *et al.,* 2006) to a strong stimulation of leaf duration, principally by delayed senescence (Karnosky *et al.,* 2005)

Forest Productivity

The individual drivers of forest productivity have shown considerable variability by species, clone, and study. A recent comparison of four long-term forest FACE studies across two continents showed a highly conserved response with an enhancement of net primary (NPP) at 560 ppm CO_2 by 23.2%, across a broad range of sites (Norby *et al.,* 2005). The authors attributed the response to increased light absorption as a result of greater leaf area index at the low end of the productivity scale and to an increased light-use efficiency at the sites with high productivity and high leaf area index (Norby *et al.,* 2005).

Modifying Factors

Genetic Variation

A wide range of inter- and intraspecific variability in response to elevated atmospheric CO_2 has been found in the forest FACE studies (Table 1). For example, in the Rhinelander study in northern Wisconsin, paper birch (*Betula papyrifera)* is the most responsive species to elevated CO_2 followed by trembling aspen (*Populus tremuloides),* while sugar maple (*Acer saccharum)* has shown no detectable stimulation in photosynthesis or growth during the nine years of the experiment (Karnosky *et al.,* 2003; 2005). A similar range of variation in growth responses has been documented within a single species for trembling aspen (Karnosky *et al.,* 2005). The wide range of variation in responses suggests that forest community change is likely to occur as atmospheric CO_2 rises and some species and genotypes are favoured over others.

Recent developments in quantitative genetics and molecular biology are allowing detailed studies to be carried out to understand the genetic variation in responses elevated CO_2. CO_2 responsiveness seems to be controlled by small changes in the expression of relatively few genes, although it is likely that these genes may be of adaptive significance and provide targets for future optimized tree breeding as climate change progresses (Gupta *et al.,* 2005; Taylor *et al.,* 2005). Studies of genetic variation in a hybrid of *Populus trichocarpa* x *P. deltoides* has allowed tree growth responses to elevated atmospheric CO_2 to be linked to specific linkage groups as quantitative trait loci (QTL, Ferris *et al.,* 2002; Rae *et al.,* 2006). For example, QTL for above-and below-ground growth stimulations in elevated CO_2 are now resolved at the level of the genome in poplar (Rae *et al.,* 2006). Using a combination of QTL analysis with rapidly developing genomic approaches, it is now possible to link these traits to specific regions of the poplar genome sequences, identifying genes of adaptive significance under future conditions of higher CO_2 concentrations.

Age

The majority of the forest FACE experiments have been conducted on trees ranging from 1 to 15 years in age. These studies have resulted in an increase in height and diameter growth, on average, of 11-16% (Kubiske *et al.,* 2006) with a mean increase in NPP of about 22% (Norby *et al.,* 2005). Particularly, responsive species such as poplars and birches can have biomass increases of 30-40% (King *et al.,* 2005; Scarascia-Mugnozza *et al.,* 2005; Liberloo *et al.,* 2006). Interestingly, there appear to be no allometric shifts caused by elevated atmospheric CO_2 as root/shoot ratios remain relatively constant (King *et al.,* 2005; Liberloo *et al.,* 2006). While these observations on young stands are particularly valuable for predicting the ability of developing young forest stands and plantations to sequester carbon under rising atmospheric CO_2, we cannot yet readily predict how older forest trees will respond from these studies.

Recently, studies of mid- to older age (Körner *et al.,* 2005; Asshoff *et al.,* 2006) forest stands suggest that these older trees do not respond to elevated atmospheric CO_2 to the extent that younger trees do. However, since the species were different to those highly responsive species summarized by Norby *et al.,* (2005), it is not possible to make a direct comparison between these studies of younger versus older trees. Since the older tree studies were done on a very limited number of trees, subjected to a step-wise increase in atmospheric CO_2, it is also not possible to extrapolate these studies to all forest ecosystems and interpret their response to the gradual increase in CO_2 that they will experience over the coming decades. Clearly, this question of CO_2 responsiveness as trees age remains an important, but unresolved, research question.

Climate

It has become very clear from the FACE experiments that the responsiveness of relative growth rates to elevated atmospheric CO_2 varies from year to year and that this variation is largely controlled by climatic conditions such as temperature, rainfall (Moore *et al.,* 2006) and incident photosynthetically active radiation (PAR: Kubiske *et al.,* 2005). The largest response of basal area increment to elevated atmospheric CO_2 in loblolly pine (*Pinus taeda)* occurred in years with the highest vapour pressure deficit (Moore *et al.,* 2006). For aspen, PAR and temperature during peak current year growth periods (*i.e.* July) and peak bud development periods (October) controlled 20-63% of the annual variation in response to elevated atmospheric CO_2 (Kubiske *et al.,* 2005).

Air Pollution

While CO_2 is rising in the atmosphere globally, other air pollutants are rising regionally across large areas in the northern hemisphere. Thus, large areas of the Earth's forests will be facing exposure to co-occurring elevated CO_2 and elevated air pollutants (Karnosky *et al.,* 2001). One of the most pervasive air pollutants is tropospheric ozone (O_3) which is common downwind of major metropolitan areas around the world. The Rhinelander FACE experiment has shown that relatively moderate levels of O_3, similar to those that already occur over vast areas of the world’s forests, can negate forest productivity enhancement induced by elevated atmospheric CO_2 (Karnosky *et al.,* 2003; 2005; King *et al.,* 2005; Kubiske *et al.,* 2006). As the IPCC has identified a rapid growth in background O_3 levels around the world, the impacts of this toxic pollutant must be factored into models of future forest productivity under rising atmospheric CO_2.

Nutrients

It has been suggested that soil fertility may constrain carbon sequestration potential in forest trees growing under elevated atmospheric CO_2 has been suggested (Oren *et al.,* 2001). Whether or not, and at what point in the life cycle of a forest, nutrient limitations will start to occur for forest ecosystems growing in enriched atmospheric CO_2 remains an intriguing question (Moore *et al.,* 2006). Interestingly, regular N additions to the three poplar species in the EUROFACE elevated CO_2 study in Italy resulted in little or no change in the response to elevated atmospheric CO_2. One possible explanation is that the EUROFACE study was developed on an agricultural soil with high nitrogen (Liberloo *et al.,* 2006).

Conclusions

Most tree species are not CO_2-saturated at current atmospheric CO_2 concentrations. Thus, it has long been predicted that forest tree carbon uptake rates will increase leading to more productive forests as atmospheric CO_2 concentrations continue to rise. However, recent studies in open-air exposure facilities suggest that elevated CO_2 effects on forest productivity are not readily predictable and can vary largely depending on tree species, age, and co-occurring stresses.

The past decade of FACE experiments has greatly refined the knowledge-base regarding the effects of elevated atmospheric CO_2 on forest tree productivity.

However, many questions remain. In this brief review, we have highlighted the following research gaps:

- A robust quantification of the CO_2 responsiveness of older forest ecosystems and of the potential for nutrient limitations to reduce forest productivity for forests exposed to elevated atmospheric CO_2 are still remaining.
- The extent to which forest productivity will be affected by interactions between elevated CO_2 and other variables is yet unclear; for example, little is known about CO_2 x temperature, CO_2 x drought, and CO_2 x forest pest and pathogen interactions. New large-scale experimentation will be required to address these questions.
- More research is necessary to identify adaptive genes of likely significance in the changing climate. Breeding and selection programs for forest trees should begin to integrate these genes identified from genomic responses of trees to elevated CO_2 into improvement programs.
- Almost no research has been done under FACE conditions for tropical

forests, which represent a large terrestrial carbon sink in the southern hemisphere.

References

Asshoff, R., Zotz, G. and Körner, C. (2006) Growth and phenology of mature temperate forest trees in elevated CO_2. *Global Change Biology* 12, 1-14.

Ferris, R., Long, L., Bunn, S.M., Robinson, K.M., Bradshaw, H.D., Rae, A.M. and Taylor, G. (2002) Leaf stomatal and epidermal cell development: identification of putative quantitative trait loci in relation to elevated carbon dioxide concentration in poplar. *Tree Physiology* 22, 63 3-640.

Gupta, P., Duplessis, S., White, H., Karnosky, D.F., Martin, F. and Podila, G.K. (2005) Gene expression patterns of trembling aspen trees following long-term exposure to interacting elevated CO_2 and tropospheric O_3. *New Phytologist* 167, 129-142.

Karnosky, D.F., Scarascia-Mugnozza, G., Ceulemans, R. and Innes, J. (eds.) (2001) *The Impact of Carbon Dioxide and Other Greenhouse Gases on Forest Ecosystems.* CABI Publishing, New York 357 pp.

Karnosky, D.F., Zak, D.R., Pregitzer, K.S., Awmack, C.S., Bockheim, J.G., Dickson, R.E., Hendrey, G.R., Host, G.E., King, J.S., Kopper, B.J., Kruger, E.L., Kubiske, M.E., Lindroth, R.L., Mattson, W.J., McDonald, E.P., Noormets, A., Oksanen, E., Parsons, W.F.J., Percy, K.E., Podila, G.K., Riemenschneider, D.E., Sharma, P., Thakur, R.C., Sober, A., Sober, J., Jones, W.S., Anttonen, S., Vapaavuori, E., Mankovska, B., Heilman, W.E. and Isebrands, J.G. (2003) Tropospheric O_3 moderates responses of temperate hardwood forests to elevated CO_2: A synthesis of molecular to ecosystem results from the Aspen FACE project. *Functional Ecology* 17, 289-304.

Karnosky, D.F., Pregitzer, K.S., Zak, D.R., Kubiske, M.E., Hendrey, G.R., Weinstein, D., Nosal, M. and Percy, K.E. (2005) Scaling ozone responses of forest trees to the ecosystem level in a changing climate. *Plant, Cell and Environment* 28, 965-981.

King, J.S., Kubiske, M.E., Pregitzer, K.S., Hendrey, G.R., McDonald,E.P., Giardina, C.P., Quinn, V.S. and Karnosky D.F. (2005) Tropospheric O_3 compromises net primary production in young stands of trembling aspen, paper birch and sugar maple in response to elevated atmospheric CO_2. *New Phytologist* 168, 623-636.

Körner, C. (2006) Tansley Review. Plant CO_2 responses: an issue of definition, time and resource supply. *New Phytologist* 172, 393-411.

Körner, C., Asshoff, R., Bignucolo, O., Hättenschwiler, S., Keel, S.G., Peláez-Riedl, S., Pepin, S., Siegwolf, R.T.W. and Zotz G. (2005) Carbon flux and growth in mature deciduous forest trees exposed to elevated CO_2. *Science* 309, 1360-1362.

Kubiske, M.E., Quinn, V.S., Heilman, W.E., McDonald, E.P., Marquardt, P.E., Teclaw, R.M., Friend, A.L. and Karnosky, D.F. (2006) Interannual climatic variation mediates elevated CO_2 and O_3 effects on forest growth. *Global Change Biology* 12, 1054-1068.

Liberloo, M., Calfapietra, C., Lukac, M., Godbold, D., Luo, Z-B., Polle, A., Hoosbeek, M.R., Kull, O., Marek, M., Raines, C., Taylor, G., Scarascia-Mugnozza, G. and Ceulemans R. (2006) Woody biomass production during second rotation of a bio-energy *Populus* plantation increases in a future high CO_2 world. *Global Change Biology* 12, 1-13.

Moore, D.J.P., Aref, S., Ho, R.M., Pippen, J.S., Hamilton, J.G. and DeLucia E.H. (2006) Annual basal area increment and growth duration of *Pinus taeda* in response to eight years of free-air carbon dioxide enrichment. *Global Change Biology* 12, 1367-1377.

Norby, R.J., Hanson, P.J., O'Neill, E.G., Tschaplinski, T.J., Weltzin, J.F., Hansen, R.A., Cheng, W., Wullschleger, S.D., Gunderson, C.A., Edwards, N.T. and Johnson, D.W. (2002) Net primary productivity of a CO_2-enriched deciduous forest and the implications for carbon storage. *Ecological Applications* 12(5), 1261-1266.

Norby, R.J., DeLucia, E.H., Gielen, B., Calfapietra, C., Giardina, C.P., King, J.S., Ledford, J., McCarthy, H.R., Moore, D.J.P., Ceulemans, R., DeAngelis, P., Finzi, A.C., Karnosky, D.F., Kubiske, M.E., Lukac, M., Pregitzer, K.S., Scarascia-Mugnozza, G.E., Schlesinger, W.H. and Oren, R. (2005) Forest response to elevated CO_2 is conserved across a broad range of productivity. *Proceedings of the National Academy of Science* 102, 18052-18056.

Oren, R., Ellsworth, D.S., Johnsen, K.H., Phillips, N., Ewers, B.E., Maier, C., Schäfer, K.V.R., McCarthy, H., Hendrey, G., McNulty, S.G. and Katul, G.G. (2001) Soil fertility limits carbon sequestration by forest ecosystems in a CO_2-

enriched atmosphere. *Nature* 411, 469-472.

Rae, A.M., Ferris, R., Tallis, M.J. and Taylor, G. (2006) Elucidating genomics regions for increased leaf growth and delayed leaf senescence in elevated CO_2. *Plant Cell and Environment*. 29, 1730-1741.

Scarascia-Mugnozza, G., de Angelis, P., Sabatti, M., Calfapietra, C., Miglietta, F., Raines, C., Godbold, D., Hoosbeek, M., Taylor, G., Polle, A. and Ceulemans R. (2005) Global change and agro-forest ecosystems: Adaptation and mitigation in a FACE experiment on a poplar plantation. *Plant Biosystems* 139, 255-264.

Taylor, G., Street, N.R., Tricker, P.J., Sjödin, A., Graham, L., Skogström, O., Calfapietra, C., Scarascia-Mugnozza, G. and Jansson, S. (2005) The transcriptome of *Populus* in elevated CO_2. *New Phytologist* 167, 143-154.

Figure 1. (A) The Aspen FACE experiment in northern Wisconsin. A control ring (B) and an elevated CO_2 ring (C) after 9 years of exposure over the entire life history of these forests.

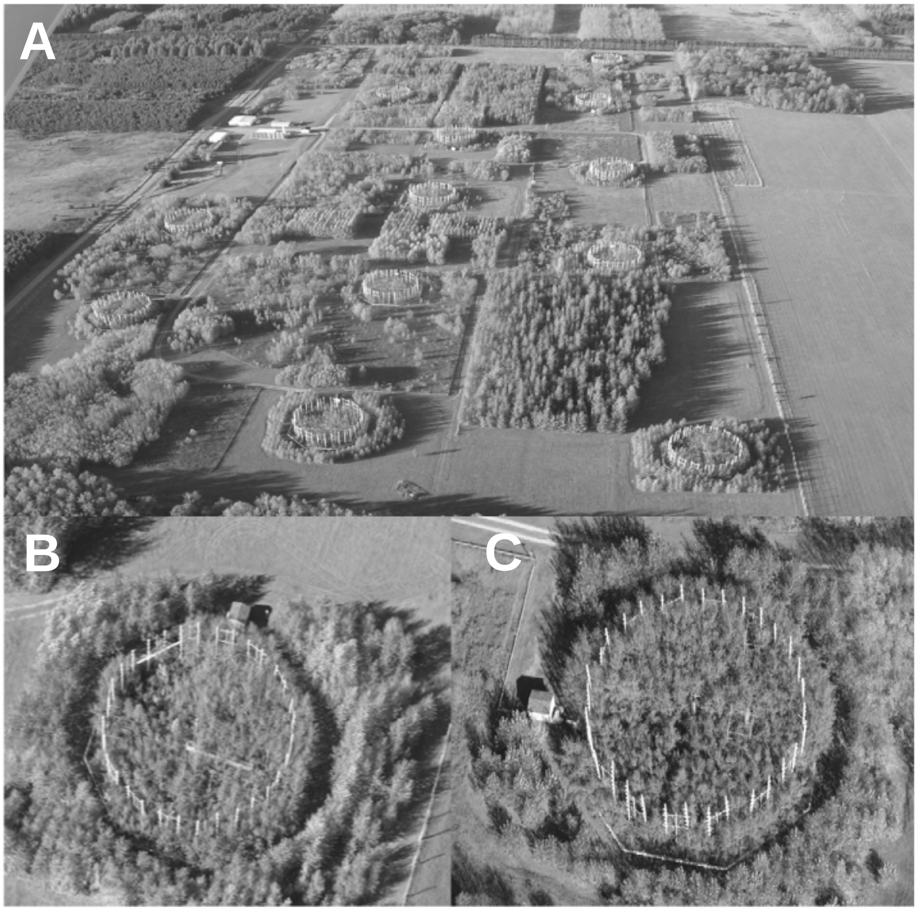

Table 1. Recent forest productivity studies in FACE experiments.

Species	Start Age (yrs)	Study Duration (yrs)	Measure	Enhancement (%)	Reference
Populus tremuloides	0	7	Total biomass	25	King *et al.*, 2005
Populus tremuloides/ Betula papyrifera	0	7	Total biomass	45	King *et al.*, 2005
Populus tremuloides/ Acer saccharum	0	7	Total biomass	60	King *et al.*, 2005
Populus tremuloides	0	7	Aboveground volume	5 to 60	Karnosky *et al.*, 2005
Betula papyrifera	0	7	Aboveground volume	68	Karnosky *et al.*, 2005
Acer saccharum	0	7	Aboveground volume	0	Karnosky *et al.*, 2005
Populus spp.	1(coppice)	3	Aboveground biomass	29	Liberloo *et al.*, 2006
Liquidambar styraciflua	10	3	Net primary production	21	Norby *et al.*, 2002
Pinus taeda	14	8	Basal Area Increment	13 to 17	Moore *et al.*, 2006
Carpinus betulus	∇1 00	4	Basal Area Increment	-13 to +13	Asshoff *et al.*, 2006
Fagus sylvatica	∇1 00	4	Basal Area Increment	5 to 50	Asshoff *et al.*, 2006
Quercus petraea	∇1 00	4	Basal Area Increment	-2 to 13	Asshoff *et al.*, 2006